Oecologia (2015) 178:943–950
DOI 10.1007/s00442-015-3268-8

CONSERVATION ECOLOGY - ORIGINAL RESEARCH

Urbanized birds have superior establishment success in novel environments

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Received: 30 May 2014 / Accepted: 6 February 2015 / Published online: 20 February 2015

Abstract Many animals have adapted to the proximity of humans and thereby gained an advantage in a world increasingly affected by human activity. Numerous organisms have invaded novel areas and thereby increased their range. Here, we hypothesize that an ability to thrive in urban habitats is a key innovation that facilitates successful establishment and invasion. We test this hypothesis by relating the probability of establishment by birds on oceanic islands to the difference in breeding population density between urban and nearby rural habitats as a measure of urbanization in the ancestral range. This measure was the single-most important predictor of establishment success and the only statistically significant one, with additional effects of sexual dichromatism, number of releases and release effort, showing that the ability to cope with human proximity is a central component of successful establishment. Because most invasions occur as a consequence of human-assisted establishment, the ability to cope

Communicated by Ola Olsson.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-015-3268-8) contains supplementary material, which is available to authorized users.

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with human proximity will often be of central importance for successful establishment.

Keywords Birds · Distance to humans · Human proximity · Human transport · Invasion · Oceanic islands

Introduction

Introductions of non-native species outside their range are common, and such invasions of novel habitats typically have dramatic consequences for native floras and faunas (Lockwood et al. 1993; Davis 2009). Numerous studies of introductions of birds to oceanic islands such as Hawaii, Tahiti and New Zealand have investigated the consequences of such releases for both introduced and native species (e.g., Veltman et al. 1996; Sorci et al. 1998; Blackburn and Duncan 2001; Blackburn et al. 2009). Many attempts of introduction were concerted efforts to bring European birds into the new environment of immigrants elsewhere (Duncan et al. 2003). There were dedicated societies in North America and New Zealand with the objective of introducing such species, thus producing a large number of replicates, where the number of releases, but also the release effort, was recorded and therefore still remains known. Studies have reported significant effects of the number of releases and release effort on success rate (e.g., Veltman et al. 1996). In addition, sexually dichromatic species tend to be less successful than monochromatic species, although the effect size is relatively small (Sorci et al. 1998). Furthermore, species with strong T cell-mediated immune responses are more successful in introduction attempts when the number of released individuals is large, but not when a small number of individuals are released (Møller and Cassey 2004). This is as expected because an infected individual is more likely to be present in a large flock of birds than in a small one (Drake 2003). Recently, Sol et al. (2012) have shown that relative brain size and the distribution of reproductive output throughout life (brood value) are the best correlates of introduction success of birds.

The ability to cope with human proximity and short flight initiation distances has a quantitative genetic basis (Møller 2014a; Lancaster 2015), and the ability of individuals to cope with human proximity can change rapidly in response to natural selection (Møller et al. 2013), as demonstrated by domesticated compared to wild species and island compared to mainland species losing their fear for humans (Cooper et al. 2014; Clutton-Brock 1987). We hypothesize that adaptation to human proximity is similar to what happened during the introductions of bird species to New Zealand and other places far from the country of origin. This process must have included initial capture of birds that were subsequently placed in cages. Initial capture is likely to have been elevated near human habitation where birds regularly encounter humans, but also where birds are abundant because of high abundance of resources in urban habitats (Møller et al. 2012). They were then transported in cages stored in a boat for many months, while being cared for by humans. Those that survived thus all had extensive experience of human proximity for a considerable amount of time. The proximity of humans typically triggers escape behavior in wild animals as mediated by corticosterone (Cooper and Blumstein 2015), and corticosterone release is known to become diminished as a consequence of the process of domestication (Clutton-Brock 1987) and urbanization (Fokidis and Deviche 2011; Partecke 2014; but see Bonier 2012 for a possible negative result) and hence the presence of humans. We suggest that birds living in the proximity of humans were predisposed for coping with capture, transport and release in the novel environment of introduction in the same way as individuals are domesticated. In contrast, species living far away from humans are less likely or unlikely to cope with capture, transport and release, and the probability of successful introduction will thus be small, simply because fewer individuals are likely to survive, and, among those that survive, individuals are likely to be more stressed.

The objectives of this study were to test if the ability to cope with the proximity of humans predicted establishment success, using introduced birds to oceanic islands as a model system. As a measure of ability to cope with human proximity, we used the difference in breeding population density between urban and nearby rural habitats. This measure of urbanization is highly consistent among cities in Europe and among years, and it is positively correlated with the known year when urbanization first took place (Møller et al. 2012). Furthermore, these two measures of urbanization are strongly correlated with two other indices of urbanization in birds (Møller 2014b). These indices of urbanization all reflect the ongoing process of urbanization (Evans et al. 2010) that started when the first commensal species such as the house sparrow *Passer domesticus* became associated with humans (Sætre et al. 2012). It is important to remember that urbanization is still ongoing, as reflected by most urban species having colonized cities quite recently Møller (2014a). This is what would be expected from most cities being of recent origin and only very recently having expanded to include half of humanity (Handwerk 2008). In that sense, urbanization is no different from any other interaction between humans and wild organisms (agriculture, forestry, fisheries and all other aspects of exploitation of the natural environment) that have all resulted in many cases of rapid evolutionary change (Hendry et al. 2008). Because previous studies have suggested that body size, relative brain size, sexual dichromatism, immune response, lifetime reproduction, habitat specialization, migration and brain size predict the probability of successful establishment in birds (e.g., Sorci et al. 1998; Møller and Cassey 2004; Sol et al. 2012), we included these additional predictors in our statistical models.

Materials and methods

Datasets

We used a database on establishment success of birds to oceanic islands (Veltman et al. 1996; Cassey 2002) that includes information on the number of releases and the number of individuals released (Electronic Supplementary Material Table S1). The 38 species included in this study were restricted to those for which we had previously and independently collected information on differences in population density between paired rural and urban habitats. Because we collected information on differences in population density between paired rural and urban habitats before we derived the predictions, our data cannot have been biased due to prior knowledge of relationships. Introduction success was quantified as the proportion of attempts that were successful. Release effort was the number of individuals released. The releases were not made in urban habitats.

We performed standard point count censuses of breeding birds to estimate urbanization, as described in Møller et al. (2012). As an estimate of relative population density in urban compared to rural habitats, we used $\log_{10}$-transformed population density of birds in urban areas minus $\log_{10}$-transformed population density in rural areas, adding a constant of 0.01 to avoid problems with a few estimates of zero. The density for each of the two habitats was the mean number of individual birds recorded per census point during the two point count censuses made in 2010. The census data show a high degree of consistency among years, and the difference in population density of birds between urban and rural sites is highly repeatable for different species across sites (Møller et al. 2012). This justifies the use of differences in population density between urban and rural habitats for the analyses. Because we found a high degree of consistency in difference in population density between urban and rural habitats, we used the mean value for the differences for our nine study sites (Rovaniemi, Finland; Oslo, Norway; Brønderslev, Denmark; Tallinn, Estonia; Poznan, Poland; Paris, France; Budapest, Hungary; and Madrid and Granada, Spain; Møller et al. 2012) as a European-wide estimate of urbanization. The difference in population density between urban and rural habitats was strongly correlated with three alternative measures of urbanization (year of urbanization, Møller et al. 2012; whether the species have at least one population with breeding population density higher than in rural populations, Møller 2014b; and whether the species breeds in urban centers; Møller 2014b), making the results independent of the actual measure of urbanization used in the present paper. We used point counts from 2010 and relate these to introductions made more than 100 years ago. This approach assumes that the measure of urbanization has remained relatively constant over time, as we found in our studies of urbanization in the same study sites in different years (Møller et al. 2012). Even if some species have become urbanized only recently, while others have been urbanized for more than 5,000 years (Sætre et al. 2012), we can still infer that extant species can be reliable classified as anciently or recently urbanized species. We also notice that urbanized species have a range of important ecological characteristics that allow for reliable classification of species as being urbanized or not (Møller 2009). Given that these characteristics pre-date any case of urbanization, they can be considered pre-adaptations for successful urbanization. We note that this approach is no different from that in the numerous other studies investigating the predictors of introduction success (review in Blackburn et al. 2009). We also note that other studies of invasions rely on the untested assumption that the predictors are reliable even though they were not collected at the same time as the response variable of invasion success (e.g., Sol et al. 2012). However, it would be difficult to explain the successful prediction of invasion success (and other comparative analyses) if such differences in timing of data collection did not have a negligible effect on the conclusions.

Sexual dichromatism was scored as a dichotomous variable with 0 being assigned to species that could not be sexed based on coloration, and 1 to species where males and females differed (see Sorci et al. 1998 for definitions and cross validations). T cell-mediated immune responses of adult birds were recorded in an extensive study of immunity in European birds, and mean estimates were derived from published data (Møller and Cassey 2004; Møller et al. 2004). Body mass was obtained from Cramp and Perrins (1977–1994). Relative brain size and brood value were from Sol et al. (2012). Relative brain sizes were the residuals of a log–log regression of brain mass on body mass, and brood value, that estimates the value of current reproduction relative to lifetime reproductive output of a species, was computed as $\log_{10}$[clutch size/(clutch size × broods per year × average reproductive lifespan)] (Sol et al. 2012). Migration distance (mean of the northernmost and the southernmost latitudes of the breeding distribution range minus the corresponding mean for the wintering distribution range) was taken from Cramp and Perrins (1977–1994). We used the habitat specialization index proposed by Julliard et al. (2006) to investigate whether difference in population density between urban and rural habitats could be predicted by specialization. This index of the diversity of habitat use

Table 1 Introduction success of birds released on oceanic islands

Variable	Sum of squares	*df*	*F*	*P*	Estimate	SE	Effect size
Intercept	0.381	1	4.70	0.038	0.268	0.124	
Difference in density	0.680	1	8.38	0.007	0.299	0.103	0.43
Release effort	0.487	1	6.00	0.020	0.000	0.000	0.38
No. releases	0.355	1	4.38	0.044	0.256	0.122	0.33
Sexual dichromatism	0.210	1	2.59	0.117	−0.186	0.116	0.26
Migration distance	0.016	1	0.20	0.661	0.046	0.103	0.07
Error	2.597	32					

The model had the statistics $F = 5.12$, $df = 5, 32$, adjusted $r^2 = 0.36$, $P = 0.0015$

has been hypothesized to reflect the degree of specialization and the underlying neural substrate linked to such specialization (Julliard et al. 2006; Ducatez et al. 2015). However, we emphasize that a recent study did not successfully link habitat generalism to technical innovation or relative brain size (Ducatez et al. 2015). The entire dataset is reported in Electronic Supplementary Material Table S1.

Statistical analyses

Statistical analyses were made with R (R Development Core Team 2014). For each introduced species, we included the following predictors: difference in density in urban and rural areas (Møller et al. 2012), sexual dichromatism (Sorci et al. 1998), PHA immune responses (Veltman et al. 1996; Møller et al. 2004), body mass (Cramp and Perrins (1977–1994), relative brain size (Sol et al. 2012), brood value (Sol et al. 2012) and migration distance (Cramp and Perrins (1977–1994). There were missing values for PHA immune response, brood value and relative brain size, therefore we started out with a full model that included all other variables with the exception of PHA immune response, brood value and relative brain size. In a second model, we added these three predictors to assess to which extent the previous conclusions were robust to the inclusion of these variables. Thus, the final models were based on full models with five predictors (difference in density, release effort, number of releases, sexual dichromatism, migration distance) or eight predictors (the five listed above and PHA immune response, brood value and relative brain mass).

Introduction success was the response variable and mean difference in density between paired rural and urban sites, release effort and number of releases were predictors. Because introduction success was estimated based on multiple introductions, we treated introduction success as a normally distributed variable in the analyses. In subsequent models, sexual dichromatism, T cell response, body mass (log-transformed), relative brain size, brood value, and migration distance were added as additional predictors to assess whether the effect of urbanization remained after controlling for the effect of these previously identified predictors. Effect sizes of significant predictors in the final model were computed from *P* values of tests following Lipsey and Wilson (2001).

Closely related species are likely to have similar degrees of invasiveness due to shared phylogenetic descent. Therefore, a phylogenetic analysis is required to control for any statistical dependence of data. Similarity in phenotype among species due to common phylogenetic descent was analysed in comparative analyses relying on a phylogenetic hypothesis (Electronic Supplementary Material Fig. S1). We used the most recent and comprehensives phylogenies available (Thuiller et al. 2011; Jetz et al. 2012) to test whether our conclusions depended on the phylogenetic hypothesis. Both were consensus phylogenies obtained from 100 trees by means of the Mesquite 2.75 software (Maddison and Maddison 2011). To control for the phylogenetic relationship among the sampled species, we used phylogenetic generalized least square regression (PGLS) models as implemented in the R statistical environment, using the libraries *ape*, *MASS* and *mvtnorm* and the function *pglm3.3.r* (see Díaz et al. 2013 for a similar approach). After testing whether the phylogenetic scaling parameter lambda (λ) differs from 0 (phylogenetic independence; Freckleton et al. 2002), we calculated the phylogenetically corrected correlation between the variables of interest after adjusting for phylogenetic effects through the estimated λ (see Díaz et al. 2013 for a similar approach and the R script).

Results

Establishment success of birds to oceanic islands was explained by a statistical model that accounted for 36 % of the variance (Table 1). The difference in density between urban and rural habitats was the most important predictor, with a statistically large effect size showing that more urbanized species were also more successfully established on oceanic islands (Fig. 1). Closer inspection of the pattern in Fig. 1 revealed equally great variation in difference in population density between urban and rural habitats across different levels of introduction success. Most species had negative differences in population density between urban and rural habitats (Fig. 1), implying that population density for most

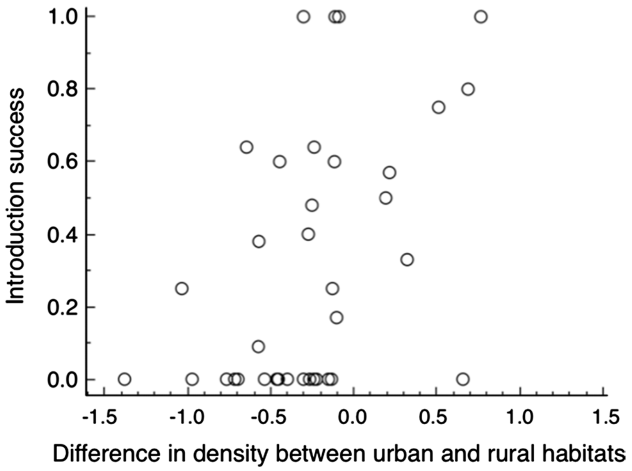

Fig. 1 Introduction success for birds on oceanic islands in relation to differences in breeding population density of urban birds minus population density of rural birds

species was greater in rural than in urban habitats. This simply reflects that there are fewer urbanized than non-urbanized species of birds, and that only a small fraction of all species have become urbanized (Møller et al. 2012; Møller 2014b). In addition, there were intermediate effect sizes for number of releases and release effort (Table 1), and low, non-significant effects of sexual dichromatism and migration distance. Results did not change when correcting for similarity in phenotype due to common phylogenetic descent, as the phylogenetic signal parameter λ did not differ significantly from zero ($\chi^2 = -0.002$, $P = 1.000$).

The effects of confounding variables were investigated in models that included body mass ($F = 0.01$, $df = 1, 31$, $P = 0.92$), PHA response ($F = 1.02$, $df = 1, 14$, $P = 0.33$), relative brain size ($F = 1.91$, $df = 1, 28$, $P = 0.18$) and brood value ($F = 3.99$, $df = 1, 28$, $P = 0.06$). None of these effects reached the level of statistical significance. The results also did not change when correcting for similarity due to common phylogenetic descent ($F = 0.03$–4.25, $P = 0.05$–0.86), as the λ parameters did not differ significantly from zero ($\chi^2 = -0.0017$ to -0.0001, $P = 1.000$). Brood value was not significantly correlated with establishment, although it had an intermediate effect size of 0.36. The results obtained with both phylogenies were almost the same, to the second decimal place (results not shown). The correlation between habitat specialization and difference in population density between urban and rural habitats was weak and not significant ($F = 0.42$, $df = 1, 85$, $P = 0.51$).

Discussion

Establishment success of birds on oceanic islands was predicted by a measure of the current extent of urbanization in the ancestral range (as reflected by the difference in breeding population density between urban and nearby rural habitats across a latitudinal gradient in Europe). The relationship between establishment success and difference in population density was not confounded by the number of releases and release effort, sexual dichromatism, PHA response, reproductive success and migration distance, that have previously been found to significantly correlate with establishment success.

Bird species with higher breeding population density in urban than in rural habitats had a disproportionately high establishment success when introduced to oceanic islands, while species with low densities in urban compared to rural habitats consistently failed when released. Successful invasions rely on transport/dispersal, establishment and subsequent expansion (e.g., Evans et al. 2010; Møller and Garamszegi 2010; Aronson et al. 2014; Sol et al. 2014). Here, we have focused on the two first components of invasion because successful establishment also includes initial transport or dispersal. Because expansion relies on successful transport/dispersal and establishment, we can infer that this should affect subsequent expansion.

Since the present study is a correlational study, we must consider whether unknown third variables may have confounded this conclusion. The number of releases and introduction effort are known to affect introduction success (e.g., Lockwood et al. 1993). Because they were included as predictors in the statistical models, these confounding variables cannot be invoked here to have caused bias. We have also shown that minor effects of sexual dichromatism and T cell-mediated immune response (that have previously been shown to be correlated with establishment success by Sorci et al. 1998 and Møller and Cassey 2004) did not affect the main conclusion from the present study. Brood value, the life-history trait that was most strongly correlated with establishment success in birds worldwide according to Sol et al. (2012), was not significantly correlated with establishment success in our case, although with a smaller effect size ($\chi^2 = 0.13$ in the present study as compared to 0.24 reported by Sol et al. 2012). Thus, this variable did not change our main conclusion that urbanization was correlated with establishment success. Sol et al. (2012) also showed a significant effect of brain size, while Maklakov et al. (2011) showed that families of birds with larger brains were more likely to have species that successfully became established in urban areas. Here, we failed to replicate such an effect, as did Møller and Erritzøe (2015) in a much larger study of brain size in urban and rural populations of the same species, and in an independent study of brain size in urban and rural species of birds.

Several previous studies have shown that pets, such as cage birds and aquarium fish or domesticated animals such as those exploited in aquaculture, have an elevated probability of becoming successful invaders (e.g., Alcaraz et al. 2005; Cassey et al. 2004; Jeschcke and Strayer 2006; Mason et al. 2013). If animals that cope with captivity are also behaviorally more flexible, they may be able to adjust to the conditions of the environment more readily. Therefore, such behavioral flexibility may facilitate establishment following release. We can dismiss this possibility because generalist species did not differ from specialists (sensu Julliard et al. 2006) in terms of differences in population density. The main result reported here is qualitatively different from these previous findings by showing that even free-living animals associated with humans enjoy an elevated probability of establishment success. We hypothesize that animals that are used to the close proximity of humans will do better on a long human-guided journey lasting several weeks when repeatedly exposed to humans than individuals that have less experience with the close proximity of humans. In addition, such individuals are also more likely to be caught and end up being transported for re-allocation elsewhere, thereby constituting a positive feedback loop.

A number of additional hypotheses may be relevant for interpreting the findings reported here. Species that are adapted to habitats modified by humans in their native range may be more successful when introduced to human modified habitats in their novel environment in accordance with the human commensalism, the pre-adaptation and the environmental matching hypotheses (Duncan et al. 2003; Blackburn et al. 2009). In addition, local biodiversity in the range of introduction has usually been reduced as a consequence of human presence providing introduced species with empty or unused niches in accordance with the biotic resistance, the habitat segregation and the niche opportunity hypotheses (Duncan et al. 2003; Blackburn et al. 2009). In fact, islands are generally more readily invaded by released species than the mainland (Sax et al. 2002), providing a general explanation for the many successful introductions on islands. Our study provided a novel addition to this line of research by emphasizing that urbanized species show a disproportionate ability to become successfully established in novel island ranges.

We suggest that the ability to cope with urbanization has hormonal, life history and behavioral underpinnings. The ability for animals to cope with human proximity can perhaps best be understood by investigating the literature on domestication and adaptation to urban environments. Domestication is known to affect escape behavior (Darwin 1868) and the underlying corticosterone level (Clutton-Brock 1987). Repeated studies of domesticated animals have shown a reduced reactivity of the stress axis compared to their wild ancestors or unselected conspecifics (Künzl and Sachser 1999; Lepage et al. 2000). A number of studies have found reductions in corticosterone levels of urban compared to rural populations of animals (Partecke et al. 2006; Fokidis and Deviche 2011; Bonier 2012; Sol et al. 2013b, 2014; Partecke 2014).

The findings reported here may be biased if the species included in this study constituted a non-random sub-sample of all species for which information on establishment success was available. Since we have included all species recorded in our point census data (Møller et al. 2012), for which information on establishment success was available, we see no reason why we should expect any systematic bias. We could by necessity only include species for which we had obtained information on urbanization. In addition, the study rests upon the assumption that the current difference in population density between urban and rural habitats even reflects past estimates of urbanization. Indeed, Møller et al. (2012) have shown explicitly that species that have been urbanized for a long time are also the species with the largest differences in breeding population density between urban and rural habitats. This makes sense because typical urban species such as rock pigeon *Columba livia*, swift *Apus apus*, jackdaw *Corvus monedula*, house martin *Delichon urbica*, robin *Erithacus rubecula*, dunnock *Prunella modularis*, chaffinch *Fringilla coelebs* and house sparrow are also the species that were already urbanized when these species were introduced to New Zealand and other oceanic islands more than 100 years ago.

The findings reported here also have conservation implications. Urbanized species are more likely to become established following successful introductions, and international trade in urbanized species is likely to result disproportionately in successful introductions. This effect is likely to be exacerbated by the fact that container ships, cruise ships and other means of transport are strongly concentrated in urban environments.

In conclusion, establishment success of birds to oceanic islands was related to an index of extent of urbanization in their ancestral range. Bird species that bred at high population density close to human habitation were much more likely to become successfully established in their introduced range, and that was the case independent of the number of introductions, the number of individuals introduced, and other potentially confounding variables. These findings suggest that cohabitation with humans is a strong predictor of subsequent establishment success.

Author contribution statement APM conceived and designed the experiments. MD analyzed the data. APM with the help of all other authors wrote the manuscript; other authors provided editorial advice.

Acknowledgments J.J. received support from the EU Regional Development Fund via the projects "Rovaniemen kaupunkilintuatlas".

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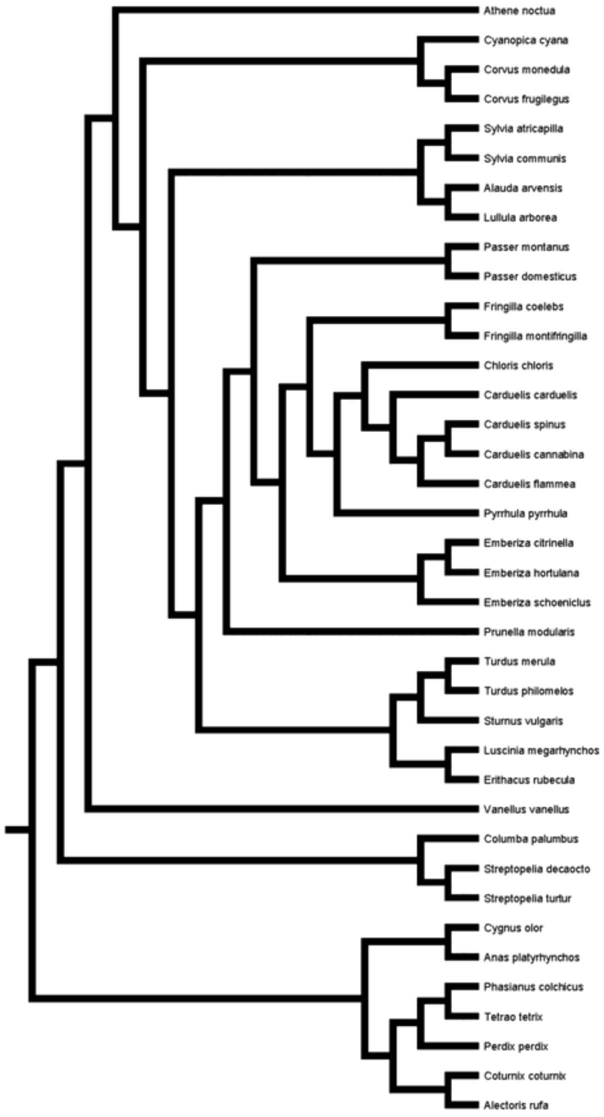
Electronic Supplementary Material Table S1. Summary information on PHA immune response in nestlings (log-transformed), difference in breeding population density between urban and nearby rural habitats, introduction success, log Body mass, log Release effort, log No. releases and sexual dichromatism (0 – monochromatic, 1 – dichromatic), brood value, habitat specialization index, log Migration distance and relative brain size. See Materials and methods for further details.

Species	PHA response	log Urban density – log Rural density	Introduction success	log Body mass	log Release effort	log No. releases	Sexual dichromatism	Brood value	log Migration distance	Habitat specialization index	Relative brain size
Alauda arvensis	-0.39	-0.65	0.64	1.56	2.44	1.15	0	-1.00	1.15	0.06	-0.42
Alectoris rufa		-0.57	0.09	2.68	1.60	1.04	1	-0.79	0.00	0.04	-2.25
Anas platyrhynchos		0.32	0.33	3.05	2.33	0.60	1	-1.49	0.96		-0.85
Athene noctua	0.24	-0.30	1.00	2.23	2.50	0.30	0	-1.19	0.00		1.10
Carduelis cannabina		-0.13	0.00	1.28	2.25	0.60	1	-1.27	0.71	-0.16	-0.27
Carduelis carduelis		-0.13	0.25	1.19	2.20	0.90	1	-1.10	0.33	-0.15	-0.27
Carduelis chloris	-0.08	0.20	0.50	1.44	2.00	0.78	1	-1.41	0.37	-0.18	-0.03

Carduelis flammea		-0.09	1.00	1.12	3.00	0.30	1	-1.33	1.02		0.09
Carduelis spinus		-0.46	0.00	1.14	1.67	0.60	1	-1.43	0.89		-0.08
Columba palumbus	0.35	-0.46	0.00	2.69	2.00	0.00	0	-1.51	0.48	-0.52	-1.80
Corvus frugilegus	0.43	0.51	0.75	2.66	2.50	0.60	0	-1.31	0.52	-0.07	1.40
Corvus monedula	0.20	0.66	0.00	2.40	1.00	0.00	0	-1.30	0.11	-0.02	1.26
Coturnix coturnix	0.11	-0.15	0.00	2.00	3.00	1.00	1	-1.04	1.01	0.18	-1.74
Cyanopica cyanus	-0.03	-1.38	0.00	1.85	1.00	0.00	0		0.00		1.69
Cygnus olor		-0.27	0.40	4.03	1.43	1.00	1	-1.44	0.32		-1.53
Emberiza citrinella	-0.19	-1.03	0.25	1.43	2.33	0.60	1	-1.41	0.76	-0.15	-0.37
Emberiza hortulana		-0.24	0.00	1.31	1.50	0.30	1		1.57		-0.42
Emberiza schoeniclus	-0.31	-0.54	0.00	1.27	2.00	0.00	1	-1.35	1.06		-0.37
Erithacus rubecula	0.00	-0.22	0.00	1.21	1.75	0.70	0	-1.54	0.78	-0.32	-0.14
Fringilla coelebs	-0.09	-0.10	0.17	1.38	2.60	0.78	1	-1.76	0.82	-0.57	-0.29
Fringilla montifringilla		-0.45	0.00	1.36	1.67	0.48	1	-1.17	1.17		-0.29
Lullula arborea		-0.72	0.00	1.48	1.00	0.00	0		0.68	-0.04	
Luscinia megarhynchos		-0.70	0.00	1.30	1.75	0.70	0	-1.04	1.52	-0.33	-0.11
Passer domesticus	0.12	0.69	0.80	1.48	2.00	1.18	1	-1.84	0.00	0.10	-0.06

Passer montanus	0.45	-0.12	0.60	1.34	1.80	0.70	0	-1.42	0.66	0.10	-0.03
Perdix perdix		-0.25	0.48	2.58	2.36	1.40	1	-0.84	0.00	0.32	-2.09
Phasianus colchicus		-0.44	0.60	3.15	2.20	1.48	1	-1.24	0.00		-1.97
Prunella modularis	0.25	-0.11	1.00	1.28	3.00	0.30	0	-1.47	1.01	-0.31	-0.24
Pyrrhula pyrrhula		-0.97	0.00	1.49	2.00	0.30	1	-1.42	0.00	0.02	0.49
Streptopelia decaocto	0.39	0.77	1.00	2.30	2.00	0.00	0	-1.80	0.00	-0.00	-1.34
Streptopelia turtur		-0.15	0.00	2.14	1.00	0.00	0	-1.42	1.43	-0.40	-1.31
Sturnus vulgaris	0.12	-0.24	0.64	1.91	2.11	1.04	1	-1.36	0.56	-0.24	0.29
Sylvia atricapilla	-0.11	-0.26	0.00	1.28	1.00	0.00	1	-1.37	1.31	-0.50	-0.32
Sylvia communis	-0.29	-0.40	0.00	1.16	1.00	0.00	1	-1.24	1.73	-0.18	-0.32
Tetrao tetrix		-0.30	0.00	3.04	2.00	0.78	1	-0.95	0.00		-1.92
Turdus merula	0.13	0.22	0.57	1.98	2.40	0.85	1	-1.82	0.70	-0.63	0.04
Turdus philomelos	0.13	-0.57	0.38	1.85	2.00	0.90	0	-1.73	1.19	-0.40	0.05
Vanellus vanellus		-0.77	0.00	2.34	2.00	0.30	1	-1.37	1.12	0.35	-0.84

Electronic supplementary Material Fig. S1. Phylogenetic relationships among the introduced species of birds.



Hypotesis 1: Thuiller et al. (2011)

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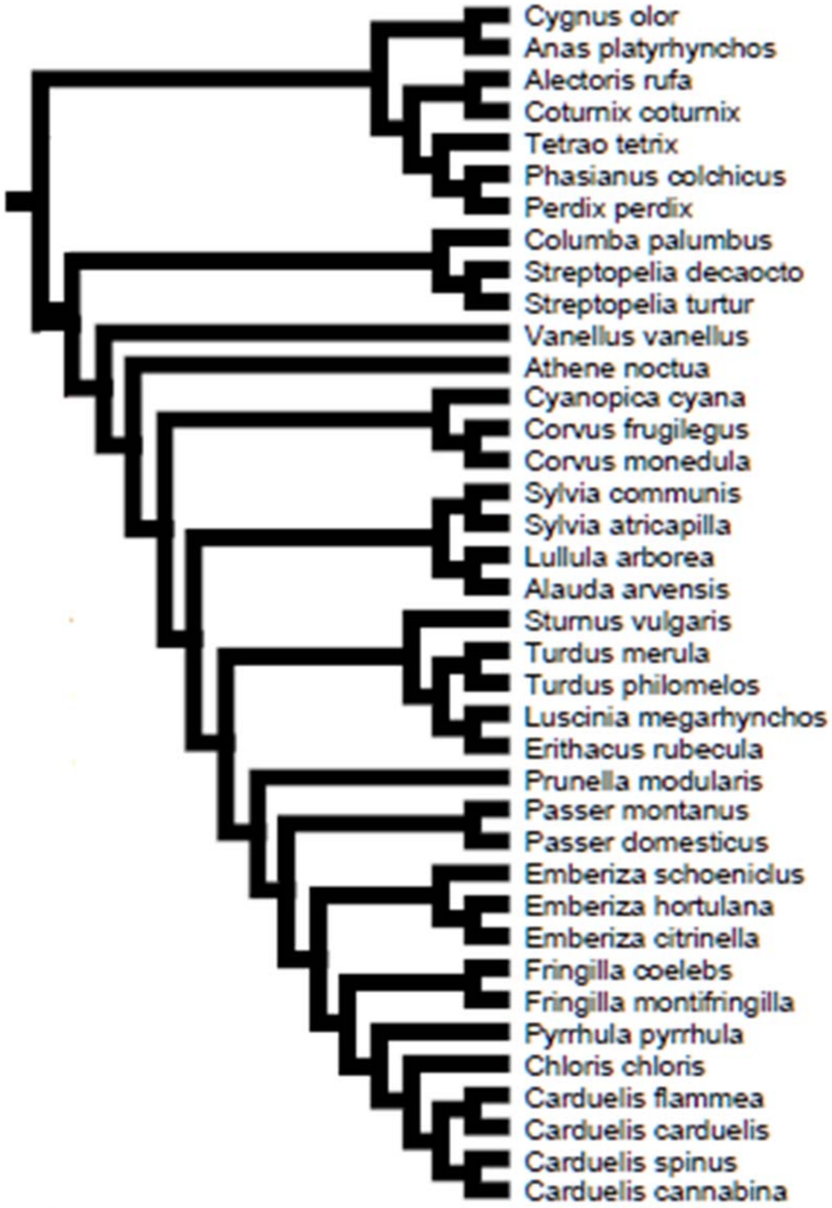

Hypotesis 2: Jetz et al. (2012)

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